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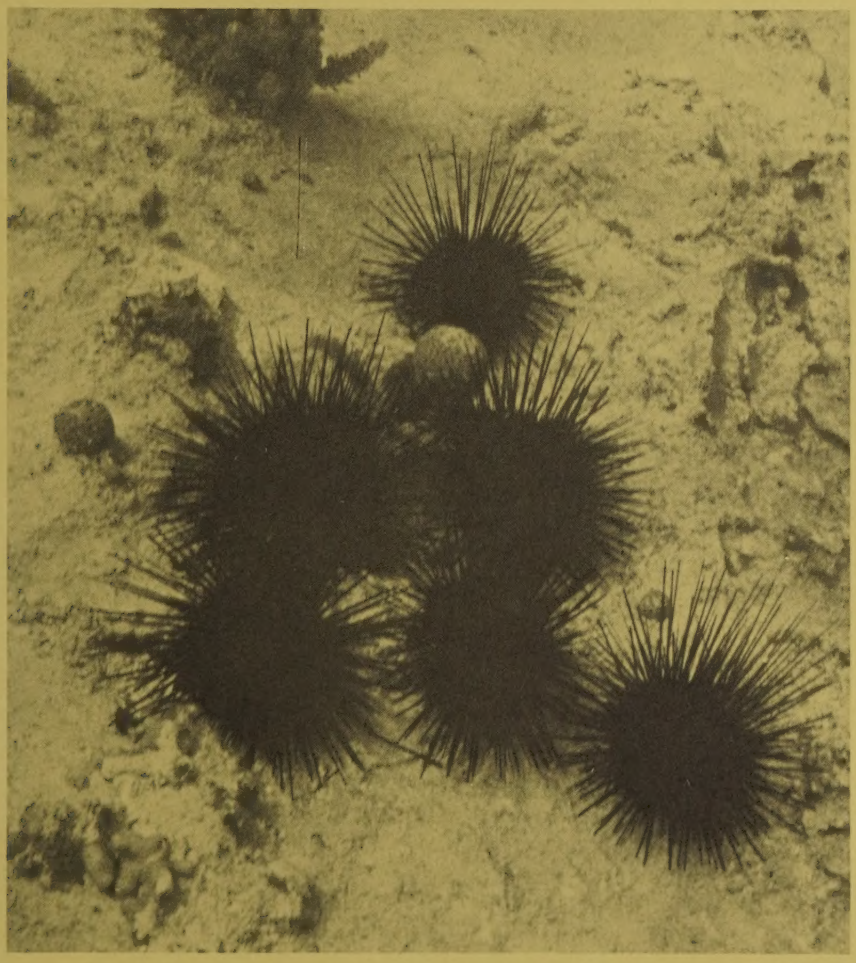
LONG-SPINED BLACK SEA URCHIN



Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers

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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida)

LONG-SPINED BLACK SEA URCHIN

by

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

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CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

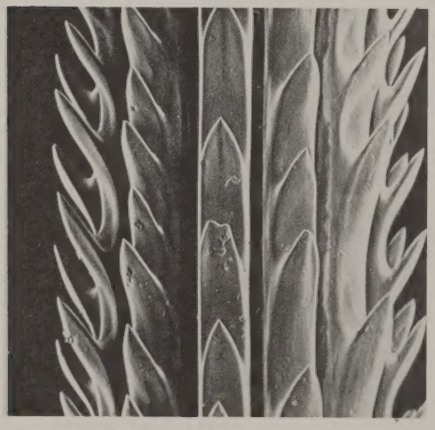
inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F - 32)	Celsius degrees

ACKNOWLEDGMENTS

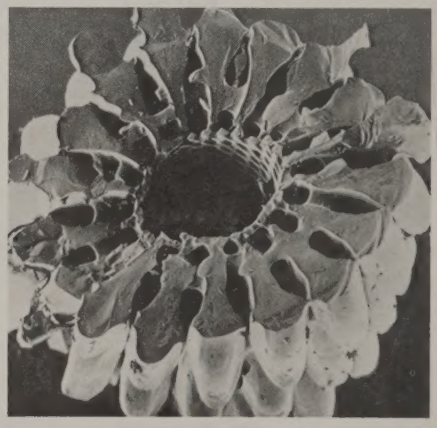
We thank John Lawrence of the University of South Florida and Robert Steneck of the University of Maine for critical reviews. John E. Miller of Harbor Branch Oceanographic Institution provided several references. Much of the research reported herein was done over the past 15 years at the West Indies Laboratory in St. Croix, U. S. Virgin Islands with the support of the National Science Foundation, the National Park Service, and the NOAA Office of Undersea Research. We also thank our colleagues, our students, and the staff of West Indies Laboratory for their ideas, assistance in field work, and logistic support. This is contribution number 164 of West Indies Laboratory, Fairleigh Dickinson University.

a. Diadema antillarum on a patch reef in St. Croix. Such high population densities were typical of many Caribbean reefs before the mass mortality of Diadema in 1983-84.

b. Diadema at the edge of a patch reef in late afternoon, beginning nightly feeding forays into surrounding seagrass beds. This feeding creates a prominent halo of grazed seagrass around the reef.

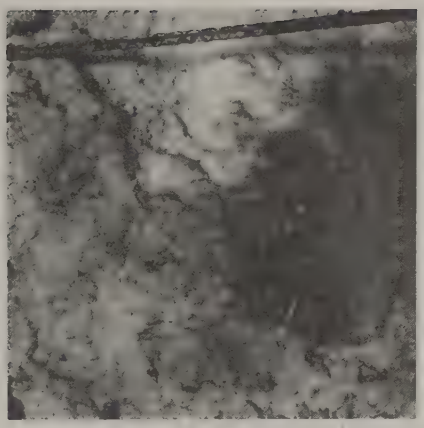


c. Scanning electron micrograph of a primary spine of Diadema (204 X), showing barbs. Spine tip is toward top of photograph.

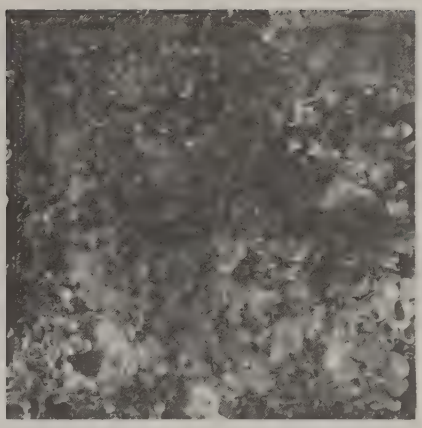


d. Scanning electron micrograph (240 X) of a section of a Diadema primary spine. Note delicateness of the spine and hollow center.

Figure 1. The natural history of Diadema.



e. Section (0.25 m^2) of a patch reef in St. Croix before the mass mortality of Diadema in 1983-84. Note paucity of algae and heavily grazed appearance of the reef surface.



f. Same patch reef section, 3 months after mass mortality. Note massive growths of benthic algae--especially the brown alga Padina.

Figure 1. (Continued).

LONG-SPINED BLACK SEA URCHIN

NOMENCLATURE/TAXONOMY/RANGE

Scientific name..... Diadema antillarum Philippi (Figure 1a,b)
Preferred common name..... Diadema
Other common names..... Long-spined black sea urchin, spiny black sea urchin, black sea egg.
Phylum..... Echinodermata
Class..... Echinoidea
Order..... Aulodonta
Family..... Diadematidae

Geographic range (Figure 2): Diadema antillarum is gregarious and occurs in almost all marine habitats including rock, coral reefs, mangroves, seagrass beds and sandy flats in the shallow coastal waters of Florida, from Pensacola on the west coast through the Florida Keys, to Cape Canaveral on the east coast. It is found on deeper reefs and rock outcrops in the Gulf of Mexico, such as the Florida Middle Grounds and Flower Gardens, to south Texas and the Yucatan Peninsula (Serrafy 1979). Diadema is abundant in the West Indies and along the north coast of South America to Surinam. It occurs in Bermuda and across the Atlantic to the Azores, the Madeira Islands, the Canaries, the Cape Verde Islands, and the Gulf of Guinea. It does not occur in the Mediterranean Sea. Diadema has been reported to depths of 400 m, but it is most abundant in shallow water (1 to 10 m) where population densities of over 20/m^2 are not uncommon (Figure 1a, b).

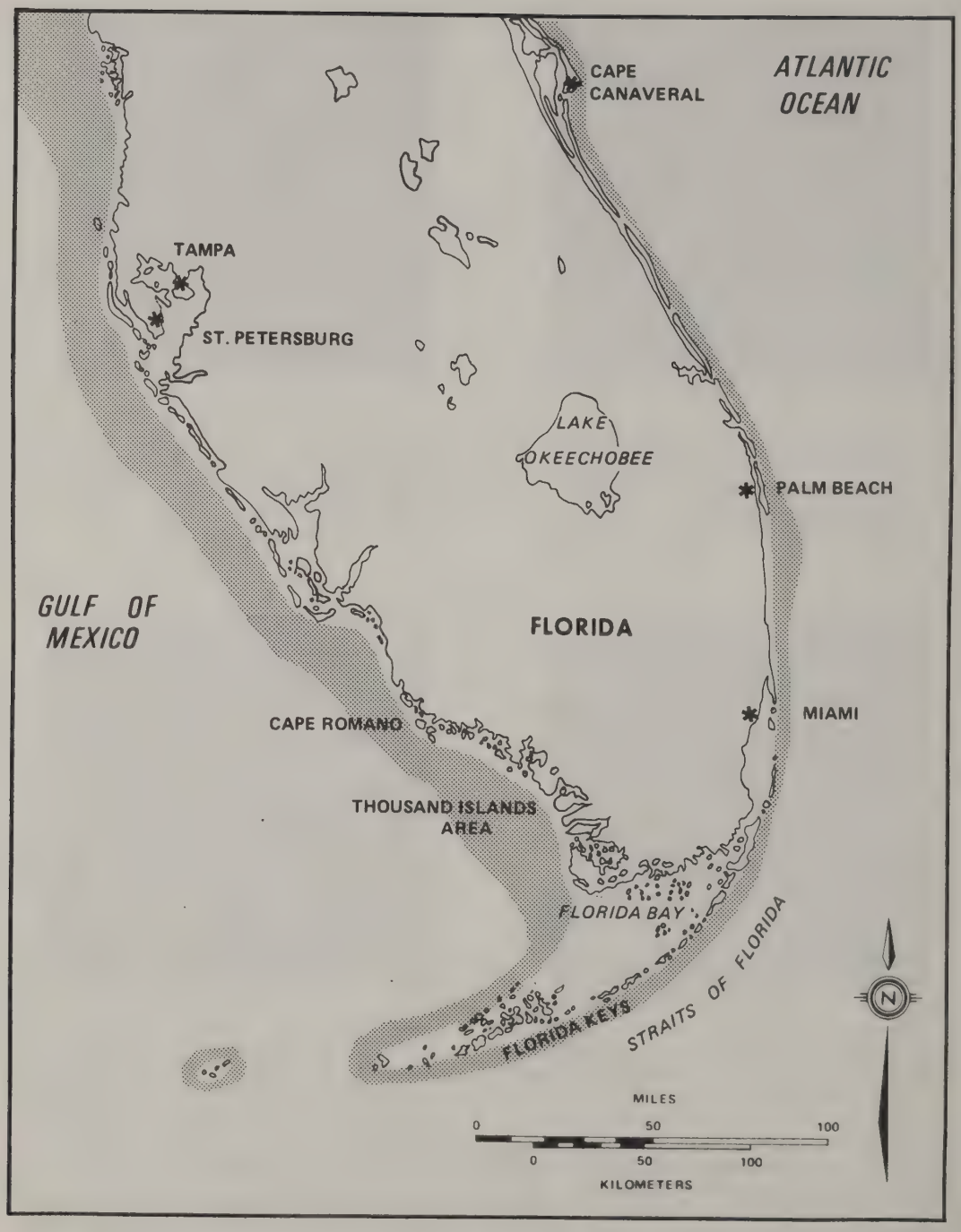


Figure 2. Distribution of Diadema in southern Florida.

MORPHOLOGY/IDENTIFICATION AIDS

Diadema antillarum is one of six species of the genus now recognized in the tropical oceans of the world (Mortensen 1940). The test of *Diadema* is circular, slightly flattened from top to bottom, and up to 10 cm in diameter; the spines are up to 30 cm long. The test is delicate and, unlike those of other sea urchins, is rarely found whole on the beach or on the bottom. In contrast to other Caribbean urchins, such as *Lytechinus* and *Tripneustes*, *Diadema* does not cover itself with pieces of vegetation, shell, or rock.

The following sections are adapted in part from Hyman (1955). *Diadema* is uniformly dark purple or almost black when mature, but in the young (to 2 cm in diameter) the spines may be banded with white. Adults occasionally have patches of white spines and very rarely are completely white. Rows of brilliant blue spots, sometimes fused into lines, may radiate from the anal region on the top of the test. These spots may be light sensors and are often hidden by dark pigment. The region around the anus (periproct) sometimes appears swollen into a bulge or finger of thin tissue called the anal cone which is apparently produced by hydrostatic pressure from the gut.

Spines

The primary and shorter secondary spines of *Diadema* are highly mobile and attached by muscles to tubercles on the test. The largest tubercles are organized into five double rows, giving the test a banded appearance. The spines are thin, delicate, and hollow (Figure 1d) containing glandular tissue that produces a toxin. The spines can penetrate human skin and sometimes break off, causing severe pain that lasts for several hours, and occasional allergic reactions. The spines are eventually absorbed by the body, or may be dissolved by the application of a mild acid such as lemon juice or vinegar. The skin may have a "tatooed" appearance from the spine pigment long after the spines are absorbed. When *Diadema* is disturbed, the spines point at the source and wave about. They are covered with small barbs (Figure 1c) directed toward the spine tip that help prevent predators from reaching the test.

Tube Feet and Pedicellariae

The other major external appendages of *Diadema* are the tube feet and pedicellariae. The tube feet penetrate the test in rows of holes that connect to the water vascular system, unique to the echinoderms. The tube feet are thin, sensitive, and capable of extreme extension. They have a terminal disc, or sucker, which enables *Diadema* to hold tenaciously to smooth surfaces. The adhesive tube feet on the lower surface of the test along with the spines are the major organs of locomotion; the tube feet on the upper surface of the test are not very adhesive and are used in respiration. The pedicellariae are morphologically equivalent to the spines and consist of a head composed of three movable jaws, mounted on a stalk that is attached to a tubercle on the test. The pedicellariae are very numerous in the area surrounding the mouth (peristome), and may be involved in food handling. They also function in defense and in cleaning the test.

LIFE HISTORY

Reproduction

Diadema becomes sexually mature at a variable size, ranging from about 3 to 6 cm in test diameter. In the Caribbean, *Diadema* have been found in spawning condition throughout

the year, though spawning appears to be concentrated from late winter to early summer (Lewis 1966). Fertilization takes place externally. Mass spawnings appear to be commonplace and may be triggered by spawning up-current that eventually spreads through a whole population. Spawning is observed when slender streams of yellowish eggs or white sperm are extruded from the top of the test from five gonopores surrounding the anus. Spawning may be induced by application of pressure to the test in the field, or by the disturbances associated with collection.

Recruitment

After a planktonic larval life of unknown duration, Diadema larvae settle to the bottom and metamorphose into tiny sea urchins. They are first seen when they attain a test diameter of about 1 cm, within 1 to 2 months after settlement. Juveniles are secretive, live under rocks and in crevices, and appear to be very vulnerable to their many fish predators. Like the adults, they are most easily seen at night, when they emerge from their hiding places to move about and feed.

Growth

Diadema grows rapidly at first--as fast as 5 mm in test diameter per month immediately after recruitment--and then gradually slows to 1-2 mm per month at a test diameter greater than 6 cm. Lewis (1966) who studied two populations of Diadema in captivity in Barbados, found that the mean monthly increment was 3.2 mm for urchins between 10 mm and 30 mm in test diameter and 1.8 mm for those of 30 mm to 50 mm. These rates are within the range found by Randall et al. (1964) in the Virgin Islands. Thus, Diadema attains a test diameter of 25-30 mm in the first year and is 45 to 50 mm in the second year. Growth rate slows markedly in urchins with test diameters greater than 6 cm and the maximum size attained by Diadema within 3 to 4 years is about 10 cm.

The size frequency distributions of Diadema measured in the field are distinctly bimodal, with a broad range in the largest size class (Lewis 1966). Given that the urchins attain maximum size within 3 to 4 years, the larger size class in any population is likely to be an accumulation of urchins 2 years old and older. Although it is not known how long Diadema lives, 4 years is a reasonable low estimate if the urchins die when growth ceases.

Behavior in Response to Light

Diadema is sensitive to light and darkness and, like many urchins, tends to be most active at night. By day Diadema usually shelters in crevices in the reef or in large aggregations in open areas. In late afternoon, the urchins become active and forage until dawn. Diadema may be active by day in areas where predators are scarce or absent.

Millott (1954) found that Diadema adapted to the dark avoids light of increasing intensity, and that light-adapted urchins move from shade into light. The nervous system in the thin skin covering the test is shielded by the pigment of superficial melanophores in light-adapted urchins. At night the pigment withdraws, exposing the nerves and the urchin becomes very sensitive to light. In late afternoon, light-adapted urchins become active and move about seeking lighted areas. They become dark-adapted during the night and seek dark shelters as the light level increases before sunrise.

Foraging Behavior

Diadema is a generalized herbivore that exploits a wide variety of plant foods (Lewis 1964; Ogden and Lobel 1978; Randall et al. 1964). *Diadema* is a grazer, scraping the hard substrate of the reef and ingesting plant material along with coral rock. It has been implicated in the bioerosion of coral reefs in the West Indies. Since stomach contents average over 90% calcium carbonate, an average population of Diadema ($10/m^2$) can produce as much as 5 kg of carbonate sediment per square meter per year by scraping the carbonate rock surfaces of coral reefs. This corresponds to about 1 cm of reef erosion per year (Ogden 1977; Stearn et al. 1977).

The foraging behavior of *Diadema* can be studied by using spine tags such as those described by Carpenter (1984). After nightly feeding forays, individuals return with remarkable fidelity to the same daytime hiding place. *Diadema* avoids grazing areas near the home crevices that have been grazed the previous night. In this way the urchins may maximize their food intake relative to the production of algae. Carpenter (1984) showed that homing correlated positively with predator abundance and negatively with urchin abundance. *Diadema* apparently senses the quality of a crevice in providing protection from predators. It vacates low-quality crevices more readily than high-quality ones when disturbed.

Diseases

Starting in January 1983 in Panama and moving through the Caribbean over the next 1½ years, populations of *Diadema* were reduced by over 90% by an unprecedented mass mortality. The mortality was first noticed near the Panama Canal and spread rapidly, following the pattern of surface currents, to Cayman, Jamaica, Mexico, Florida, and Bermuda. Urchins also died along the north coast of South America and through the Lesser Antilles (Figure 3). The mortality was most likely caused by a pathogen, rather than pollution or an oceanographic event such as elevated water temperature. The evidence for a species-specific disease pathogen is that only one species of urchin was affected, and the mortality did not diminish in severity over long distances (Lessios et al. 1984a; Hunte et al. 1986).

The first manifestation of the disease was sediment sticking to the normally purple-black spines. Although it was difficult to observe, the urchins at this point had already stopped feeding and moving about the reef. Patches of skin and spines sloughed from the test, and the urchins were rendered vulnerable to attack by predators. Once bare, whitish patches appeared on the test, urchins died within approximately 4 days.

Some individuals survived. Many of these had short, stubby spines where fish had bitten off diseased spine tips in futile efforts to prey on the urchin. The stumps of the old spines rapidly regenerated new, sharp tips.

Although the cause for the epidemic remains unknown, this event, which is unprecedented in scale and severity for a tropical marine organism, has provided a great natural experiment. *Diadema* was one of the most abundant organisms in the Caribbean region. In the next section, the events on Caribbean reefs following the mortality are described.

ECOLOGICAL ROLE

Associated Organisms

The young of a number of species of fishes take shelter in the spines

Figure 3. The tropical western North Atlantic. Diadema is distributed throughout this region. Arrows indicate the prevailing surface currents and the letters show the track of the mass mortality at nine sites: A, Panama, January 1983; B, Cayman, June 1983; C, Jamaica, July 1983; D, Columbia, August 1983; E, Mexico, July 1983; F, Florida Keys, July 1983; G, Curacao/Bonaire, November 1983; H, Barbados, October 1983; and I, Virgin Islands, January 1984 (after Lessios et al. 1984a).

of Diadema; these include grunts (Haemulidae), drums (Sciaenidae), wrasses (Labridae), and butterflyfishes (Chaetodontidae). Some adult fishes, particularly the cardinalfishes (Apogonidae), have been seen within the spines. Small mysid shrimps (Mysidium) also shelter in the spines, and the flattened urchin crab, Percnon gibbesi, is often found under Diadema in the West Indies. Two undescribed species of palaeomonid shrimps have been found living as commensals among the spines in the Lesser Antilles, but not in Florida. Both species match the color of the spines and are almost impossible to see until they are removed from urchins held in aquaria (Randall et al. 1964).

Predators

Although direct observations of predation on Diadema are few, evidence of predation, such as crushed tests and spines, is not uncommon. The known predators of Diadema include wrasses (Labridae), triggerfishes (Balistidae), grunts (Haemulidae), porgies (Sparidae), porcupinefishes (Diodontidae), and toadfishes (Batrachoididae), as well as the large king helmet snail, Cassis tuberosa (Randall 1967; Hoffman and Robertson 1983). Territorial damselfishes often attack Diadema and bite their spines; this behavior is aggressive, not predatory (Williams 1981). Although Quinn (1965) reported cannibalism in Diadema, it occurred in an aquarium and probably does not happen naturally.

Randall (1967) listed 15 species of fishes in which echinoid remains comprised more than 5% of the gut contents. The queen triggerfish, Balistes vetula, appears to be the most important of these predators; 73% of the gut contents consisted of echinoids, primarily Diadema. Triggerfish blow a jet of water at the base of the sea urchin to dislodge it, then attack its oral side where its protective spines are shorter and the peristomial membrane surrounding the mouth provides a soft point of attack. Other fish predators apparently crush the urchins or repeatedly bite off the longer spines until a crushing bite of the test can be taken. For wrasses, grunts, and porgies, Diadema makes up a smaller proportion (5-45%) of the diet.

The king helmet snail inhabits seagrass beds and sandy edges of reefs where it can be an important sea urchin predator. Although Diadema is not its preferred prey, the king helmet occasionally attacks and consumes it (Schroeder 1962). The snail locates its prey by chemoreception and rapidly crawls over the test, punctures it with the radula, and consumes the inner tissues (Hughes and Hughes 1971). Diadema in aggregations show an alarm response--the individuals move rapidly apart if one of their number is injured. They will also move away from water conditioned by potential predators (Snyder and Snyder 1970).

The apparent role of predators in controlling population sizes of Diadema is based mainly on correlative evidence. Over large areas of the Caribbean there is a negative correlation between population densities of Diadema and the abundance of sea urchin predators, mainly the queen triggerfish (Hay 1984). Predation pressure is implicated in determining the nocturnal and homing behavior of Diadema. High predation pressure requires sea urchins to have hiding places during the day, and thereby introduces a habitat factor into the control of Diadema population sizes. Reef areas with high spatial heterogeneity that provides greater protection from predators probably maintain the higher population densities of sea urchins, irrespective

of the abundance of predators (Sammarco 1982).

Many of the predators of Diadema are preferred food fishes and are easily caught by fish traps or by spear. Inasmuch as fishing pressure on many Caribbean reefs is high and the fish stocks are moderately to severely overfished, it is possible that the populations of Diadema were unnaturally high before the mass mortality described earlier (Woodley 1979).

Interactions with Seagrass-Beds and the Algal Community

Some of the earliest studies of herbivores on coral reefs in the Caribbean demonstrated that grazing by Diadema resulted in a low standing crop of benthic algae (Randall et al. 1964), and this grazing has been experimentally demonstrated to be a primary factor in keeping the benthic algal community in a low biomass, high turnover state (Ogden et al. 1973; Sammarco et al. 1974; Carpenter 1981, 1986; Sammarco 1982). Typical algal biomass values for areas grazed by sea urchins range from 10-40 g/m^2 (decalcified dry wt.). If Diadema is experimentally excluded from reef areas that remain available to herbivorous fishes, algal biomass can exceed 150 g/m^2 (Carpenter 1981, 1986; Sammarco 1982). High algal biomass (>1 kg/m^2) is characteristic of areas where Diadema and other herbivores are excluded naturally by wave action, such as the tops of algal ridges and shallow wave-washed beachrock, and of areas relatively inaccessible to sea urchin grazing, such as crevices and vertical surfaces. These refuges create a mosaic of algal biomass over the reef surface. Patches of higher algal biomass also result from the exclusion of Diadema by territorial damselfishes (Brawley and Adey 1977; Sammarco and Williams 1982).

Similar effects of Diadema grazing on plant biomass have been demonstrated in seagrass beds (Ogden et al. 1973). Sea urchins inhabiting the margins of reefs migrate at night into the surrounding seagrass beds and create halos adjacent to reefs by consuming seagrasses and rhizophytic algae (Figure 1b). Halos are also maintained by grazing fishes near reefs by day, and possibly by the physical action of waves and currents, particularly during periodic storms (Randall 1965; Tribble 1981).

Grazing by Diadema also affects the species composition of the benthic algal community (Sammarco et al. 1974; Carpenter 1981, 1985, 1986; Sammarco 1982). Four months after the removal of all Diadema from a patch reef in St. Croix, the algal community was dominated by a few large algal species that were previously rare or absent, including Padina jamaicensis (P. sanctae-crucis), Turbinaria turbinata, Jania adherens, and Dictyota spp. (Sammarco et al. 1974). Similar shifts in algal species composition have been demonstrated when Diadema population density was manipulated experimentally. Algal communities subjected to moderate to intense grazing by Diadema are dominated by filamentous species of algae that are structurally simple and have high growth rates. These algal assemblages, commonly referred to as "algal turfs," consist of 20-50 species/m^2, including representatives from five algal divisions (Cyanophyta, Chrysophyta, Chlorophyta, Phaeophyta, Rhodophyta). Under the highest grazing intensities, the algal community becomes dominated by crustose coralline algae that are able to withstand the intense scraping of sea urchin grazing (Carpenter 1981; Steneck 1982).

Most substrate on coral reefs is occupied, so space may be a factor potentially limiting algal populations

there. Thus, algae may exhibit interspecific competition for space unless the competitive dominants are controlled by herbivores. When Diadema is removed, algal species normally unable to coexist with Diadema become dominant. Eventually, if herbivorous fishes are also excluded, the large brown algal taxa Sargassum spp., Turbinaria turbinata, and Padina jamaicensis dominate. It is highly improbable that, when all herbivores are excluded, the new dominant species of algae are just colonizing bare substrate and not competitively displacing other species of algae; this is because bare substrate is so rare (and may be even rarer when grazers are absent). Areas accessible to herbivorous fishes but not to Diadema have often become dominated by the brown filamentous alga Sphacelaria tribuloides (Carpenter 1986). This alga may be a competitive dominant that is avoided by fishes (possibly because it contains a disagreeable chemical) but controlled by Diadema. Alternatively, Diadema may control S. tribuloides, but when urchins are absent and herbivorous fishes are present, other algae which are competitively dominant over S. tribuloides and controlled by Diadema may be controlled by the fishes; S. tribuloides can then flourish. The successional sequence and the particular species that make up algal communities released from sea urchin grazing depend partly on spore availability and the previous presence of juvenile plants within refuges.

Grazing by Diadema has also been shown to have dramatic effects on algal community metabolism (Carpenter 1981, 1986). Although algal communities grazed by Diadema had biomass values as low as 10% of those not grazed by sea urchins, productivity (as measured by changes in dissolved oxygen) per unit area was not lower than in nongrazed areas. When productivity is expressed on a per unit algal biomass (chlorophyll a) basis, algal communities grazed by Diadema are 3-5 times more productive than those not grazed by Diadema (Carpenter 1986). This greater productivity may be the result of a reduction in the algal "canopy height," which may allow for more efficient use of incident irradiance by epilithic and endolithic algal turf species.

Another explanation, not mutually exclusive, is that nitrogenous excretions from Diadema supply an additional nutrient source to grazed algal turfs, and thereby increase their biomass-specific productivity. Excretions originate from the respiratory surfaces, including the gills, on the underside of the urchin. Nutrients excreted into a restricted volume of water under the urchin may be retained and concentrated and allow sufficient time for algal uptake. Species of phytoplankton are known to take up nutrient pulses that exceed their immediate metabolic demands and store them for later use (Lehman and Scavia 1982). Since algal-covered substrata within sea urchin feeding ranges are repeatedly grazed, the input of nitrogenous excretions may provide a predictable source of nutrients in an environment that is characteristically nutrient-poor. Preliminary estimates of ammonium excretions from Diadema and the nitrogen requirements of algal turfs (based on known primary productivity rates and carbon: nitrogen ratios of algal turf species) suggest that excreted ammonium could supply up to 31% of the nitrogen required (E. Telemaque, S. L. Williams, and R. C. Carpenter, unpubl. data). Further experiments are needed to elucidate the mechanisms responsible for the increased biomass-specific primary productivity exhibited by algal turfs grazed by Diadema.

Interactions with Algal Community after Mass Mortality

After the mass mortality of Diadema in 1983-84, changes in the algal community that were predicted by previous experiments in which Diadema was excluded occurred in the reef areas studied. Algal biomass increased dramatically in Jamaica (Hughes et al. 1985; Liddell and Ohlhorst 1986); Curacao (Bak et al. 1984); Panama (Lessios et al. 1984b); Puerto Rico (Ballantine 1984); and St. Croix (Carpenter 1985). In St. Croix, areas previously grazed by Diadema supported algal communities with biomass values 5-20 times higher than those present before 1983 (Figure 1e, f). Algal biomass on several reefs in the Florida Keys appeared to undergo a less marked increase, suggesting that Diadema was not the dominant herbivore before the mass mortality (M. E. Hay, University of North Carolina, Morehead City; pers. comm.).

Changes in algal species composition also occurred after the die-off. Reefs in Jamaica became dominated by the brown algae Lobophora variegata and Dictyota spp. (Liddell and Ohlhorst 1986). Lessios et al. (1984b) also reported that shallow reef areas in Panama became covered with Dictyota. One week after the mortality of sea urchins in St. Croix, juvenile forms of the macroalgae Acanthophora spicifera and Laurencia obtusa were evident within the algal turf communities. Six months after the die-off, several macroalgal species were predominant members of the algal community including Dictyosphaeria cavernosa, Dictyota spp., Lobophora variegata, Amphiroa fragilissima, Jania adherens, and Laurencia obtusa. Two years after the mass mortality, many reef areas were dominated by the leathery macroalgae Turbinaria turbinata and Sargassum spp. (Carpenter 1985).

The mass mortality of Diadema had significant effects on the primary productivity of algal communities on reefs as well. Five days after the mortality event, primary productivity per unit area had decreased by 33%, even though algal biomass had increased by 27% over the same period. The decrease in primary productivity per unit algal biomass was even sharper, dropping by 60%. After the initial decrease, productivity remained low and was characteristic of levels in algal communities grazed only by herbivorous fishes before the sea urchin mortality (Carpenter 1985; 1986). These patterns were most evident in the reef zones where Diadema was previously most abundant.

The results of this "natural experiment" confirm that grazing by Diadema is a primary structuring force in maintaining algal abundance and community structure on reefs and support the hypothesis that Diadema has a positive effect on the primary productivity of algal communities on reefs.

Interactions with Other Echinoids and Herbivorous Fishes

Potential competition for food resources between Diadema and other herbivores has been investigated experimentally only for a few species. Williams (1980, 1981) and Sammarco and Williams (1982) investigated the relationships between Diadema, the threespot damselfish (Stegastes planifrons) and the sea urchin Echinometra viridis in Jamaica. Territorial damselfish apparently mediated the competition between Diadema and Echinometra by altering the spatial distribution of the two sea urchin species. Damselfish attacked Diadema that attempted to enter their territories during the day and restricted them to the edge of the damselfish colonies. Echinometra distributed within the colonies and thereby had access

to algae that were not available to Diadema. Competition between damselfish and Diadema was not eliminated by the territorial behavior of the fish, since sea urchins frequently grazed the algal lawn at night when the resident fish were inactive. Experimental additions of both sea urchin species to patches that damselfishes had been removed from indicated that, under the population densities tested, competition occurred in the absence of damselfish mediation.

Lessios et al. (1984b) reported that populations of Echinometra viridis in Panama increased shortly after the die-off of Diadema in shallow reef areas, and suggested that a release from competition may have been the cause. Likewise, populations of the sea urchin Tripneustes ventricosus in Jamaica and in some localities in St. Croix appeared to increase and move into reef zones where they were not present (or abundant) before the Diadema mass mortality. No increases in abundance of populations of E. viridis were noted in St. Croix (R. Carpenter, unpubl. data).

The population sizes of sea urchin species may often be primarily controlled by factors other than competition (e.g., recruitment). But intraspecific competition probably has a very important influence in controlling the population size of Diadema. There is a strong inverse correlation between mean individual size and population density (Carpenter 1981), suggesting that food availability significantly affects individual sea urchin size and probably reproductive output. Because agonistic behavior has not been observed in Diadema, intraspecific exploitative competition for food (and the subsequent allocation of energy into reproduction) probably limits the maximum population density in the absence of predators.

Investigators have addressed potential competition between Diadema and several species of herbivorous fishes. Ogden et al. (1973) noted increases in the population sizes of juvenile parrotfishes and surgeonfishes after removing all Diadema from a patch reef in St. Croix. Hay and Taylor (1985) experimentally removed Diadema from a section of a reef in St. Thomas, U. S. Virgin Islands, and compared the grazing intensity and population densities of herbivorous fishes with those in an adjacent control reef. As upright algae increased after the sea urchin removal, herbivorous fishes grazed more intensively. Four months after the sea urchin removal, local densities of parrotfishes had increased in the removal area by 450%, probably through migration from adjacent reef areas.

Data on grazing intensity (measured as bites per unit of area per unit of time from time lapse movies) and population densities of herbivorous fishes on a reef in St. Croix, both before and after the mass mortality of Diadema, also suggested that competition for algal resources occurred before the die-off (Carpenter 1985, 1986). Within a week after the mass mortality, grazing intensity by herbivorous fishes in a backreef and reefcrest area increased by 400%. Grazing intensity thereafter remained elevated (but the variance for these data is high). Population sizes of parrotfishes and surgeonfishes increased significantly within 9 months after the die-off and continued to increase thereafter. Since the sea urchin mortality occurred over a wide range of habitats, the increase in population sizes of herbivorous fishes is probably not a result of migration. Many of the fishes censused, particularly the surgeonfishes, were juveniles, suggesting that population increases were due to either increased recruitment of larvae from the plankton or increased

post-larval survival. These patterns in both grazing intensity and population size were most pronounced in shallow reef zones where Diadema was previously most abundant.

Role in Controlling Coral Reef Community Structure and Function

Grazing by Diadema disturbs the benthic reef community. Substratum grazed by Diadema is bared for either colonization by larvae or spores or for growth of established organisms from the perimeter. As in disturbances in other environments, the variables important in determining the fate of opened substratum are the intensity (i.e. size) of the disturbance and the frequency of its occurrence (Levin and Paine 1974).

Benthic algae are the primary food source of Diadema, although other benthic sessile organisms are occasionally consumed (Bak and van Eys 1975; Carpenter 1981). Most reef algae require a hard substratum for attachment, which most frequently consists of skeletons of scleractinian corals. Benthic algae are also among the fastest growing reef organisms, which enables them to rapidly invade substratum opened by grazing. Several studies have demonstrated that grazing of algae by Diadema allows the settlement and survival of coral spat (Sammarco 1980, 1981). The removal of grazing Diadema leads to decreased survival of settling corals, and to increased mortality of larger colonies that are abraded by large algal species such as Turbinaria turbinata and Sargassum spp. At high population densities of Diadema (greater than 10-12 individuals/m^2) intense grazing may have a similar negative effect, the coral spat being indiscriminantly grazed and larger coral colonies being undercut by extensive bioerosion (Ogden 1976; Sammarco 1980). At intermediate sea urchin densities (6-8/m^2) the algal community is sufficiently disturbed to allow increased survival of coral species and probably other benthic sessile organisms.

Grazing tends to maintain areas dominated by turf algae between individuals and colonies of benthic sessile invertebrates that compete for space when they are adjacent. Depending on a variety of factors, including possible dominance hierarchies (or competitive loops), competition between adjacent sessile invertebrates often leads to a reduction in the number of species coexisting in an area. Intermediate grazing intensity by Diadema reduces the frequency of such contacts and thereby appears to have a maximizing effect on both the diversity of benthic sessile invertebrates and algae (Carpenter 1981; Sammarco 1982).

Grazing by Diadema may have a similar effect on the metabolism of whole reef systems. It is clear that productivity is much higher on reefs dominated by algae than on reefs dominated by corals (Smith and Marsh 1973; Adey and Steneck 1985). Several factors influence the relative coverage of these reef components: age of the reef, exposure to waves and swells, degree of spatial heterogeneity, and historical factors. Given a reef of intermediate age (e.g. 3000-5000 years), and taking spatial heterogeneity into account, benthic algal turfs cover 50% to 80% of the reef surface (Adey and Steneck 1985). Algal turfs are the most productive component of coral reefs and are responsible for an average of 70% of total reef primary productivity. Since Diadema grazing results in the maintenance of algal turfs and has the demonstrated effect of increasing their rates of primary productivity, the presence of Diadema on coral reefs results in an overall increase in whole reef primary productivity. Although the fate of this increased

productivity has not been experimentally determined, it is likely that greater secondary production also results.

Through direct effects on algal communities or indirect effects on other benthic reef organisms, grazing by Diadema is a major factor controlling the community structure and function of coral reefs. Although many questions about the ecology of Diadema remain, results from over 20 years of experiments and observations, plus the confirming results after the 1983-84 mass mortality in the Caribbean, indicate that perhaps no other single species in the coral reef environment has such profound effects on the other organisms composing the reef community.

ENVIRONMENTAL REQUIREMENTS

Diadema requires relatively clean, highly oxygenated, circulating water. It is most abundant on hard coral reef or rock surfaces where wave action is light to moderate, but is often found on lagoonal sandy bottoms or in seagrass meadows. Like most coral reef organisms, Diadema has a narrow range of tolerance to changes in temperature and salinity. It is sensitive to desiccation and is rarely found in areas that are exposed at low tide. Diadema avoids still, shallow water that may become superheated (above 35°C) during the day. It is not found near the mouths of rivers and streams or on reef flats where the seawater may be diluted to a salinity of less than 30 ppt by runoff or periodic rainstorms. Diadema is difficult to keep in aquaria and will die in a short time after collection if kept in a crowded container.

Diadema densities can be high in the vicinity of sewage outfalls (J. C. Ogden, personal observations). This may be a result of nutrients simulating algal growth or of direct uptake of dissolved organic material by the urchin.

One of the major effects of development in the Caribbean is uncontrolled sedimentation from the runoff of cleared lands or from dredging. Diadema appears to be more tolerant to sedimentation than corals, but will disappear from areas where sedimentation is heavy. Sediment affects urchins by abrasion, smothering, and by cutting off light necessary for algal growth.

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, morphology, range, life history and environmental requirements of coastal aquatic species. They are designed to assist in environmental impact assessment. The long-spined black sea urchin, Diadema antillarum, is one of the most common marine invertebrates in the South Florida and Caribbean regions. Diadema is gregarious and is found in large groups on hard bottom in shallow waters. Spawning is year-round, concentrated in late winter to early summer, and the larvae spend an unknown period in the plankton. Following settlement, growth is rapid, to a maximum size of about 10 cm in 3 to 4 years. Diadema is a grazer, feeding on small algal filaments and on seagrass, and tends to be active at night. Grazing activities can produce grazed halos around patch reefs in the vicinity of seagrass beds. Many experiments have indicated the importance of this grazing in the coexistence of species on the reef and in maintaining high biological productivity. In 1983-84, Diadema suffered an unprecedented mass mortality and its populations were reduced by up to 98% throughout its range. The elimination of Diadema has affected algal biomass, reef productivity, and fish populations. Diadema populations are slowly beginning to increase, but complete recovery may take years.

17. Document Analysis a. Descriptors
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